SHORT COMMUNICATION

Evaluation of Factors Causing Reflectance Differences between Sun and Shade Leaves

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Shade and sun leaves of Valencia orange [*Citrus sinensis* (L.) Osbeck] were collected to evaluate comparative effects of their leaf chlorophyll concentration, water content, thickness, and mesophyll volume of air on visible light reflectance, specifically the 0.45-, 0.55-, and 0.65-μm wavelength (WLs). The reflectance at the 0.45-, 0.55-, and 0.65-μm WLs of sun leaves but not shade leaves was negatively correlated with total chlorophyll concentration. Reflectance at the 0.45-μm WL was affected by leaf water content for both sun and shade leaves. Sun leaf reflectance at the 0.45-μm WL, but not shade leaf reflectance was affected significantly by leaf mesophyll air volume. The effect of leaf thickness on reflectance was apparently of less importance than that of the chlorophyll content, air volume, and water content. The influence of shade and sun leaves on visible light reflectance/absorptance of at least Valencia orange tree canopies probably should be considered in modeling canopy reflectance and growth.

Introduction

Earlier studies by the author (unpublished data) indicated that sun leaves of the avocado tree (*Persea americana* Mill.) had different reflectances over the 0.5–2.5-μm waveband than did shade leaves. At the 1.0-μm near-infrared wavelength (WL), old sun leaves with well-differentiated and lacunose mesophylls had the most reflectance (50.7%), new shade leaves had intermediate reflectance (43.9%), and new sun leaves with compact mesophylls had the least reflectance (30.1%). Reflectance differences between the sun and shade leaves were also present within the 0.5–0.75-μm portion of the visible light waveband. At the 0.55-μm green light reflectance peak, for example, new shade leaves with less total chlorophyll concentration had more reflectance than either old or new sun leaves with more chlorophyll. Reflectances of the old and new sun leaves were essentially the same at the 0.65-μm WL.

Shade leaves are thinner than sun leaves with a greater volume of mesophyll air space, thinner palisade cells, and fewer stomata (Sharma and Sen, 1971). Leaves differentiating in the shade have a weaker development of palisade tissue (Esau, 1965) than leaves exposed to light during differentiation (sun leaves). Thus, differences in mesophyll structure occur in leaves at different levels of the same plant because of variable light conditions that occurred during leaf development and may cause differences in leaf optical characteristics.

Plant canopies with a preponderance of shade leaves would probably have a different signal for remotely used sensors than canopies with more sun than shade leaves. Moreover, a sensor's signal would be probably affected by its position relative to canopies as to whether it is receiv-

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ing radiation from the side of the canopy that normally receives full sunlight (sun leaves) or from the side that receives partial sunlight (shade leaves).

Our primary objective, therefore, was to study the reflectance of shade versus sun leaves of Valencia orange trees within the visible light spectrum in relation to the leaves' morphological and physiological parameters.

Materials and Methods

Ten sun and 10 shade leaves of Valencia orange [*Citrus sinensis* (L.) Osbeck] trees were collected for each of 4 days from a different tree for each day. After harvest each day, leaves were placed in plastic wrap tightly to inhibit dehydration and stored on ice immediately for transport to the laboratory. A number was assigned to each leaf, and then leaves were randomly selected for measurements: five for total leaf chlorophyll assay and spectral analyses, and five for leaf water content, thickness, area per leaf, and percent of leaf volume determinations. Except for percent of leaf volume, all measurements were made following procedures used by Gausman et al. (1970, 1971): A Beckman Model DK-2A,[1] equipped with a reflectance attachment, was used to measure total diffuse reflectance over the 0.5–0.75-μm waveband on upper (adaxial) surfaces of single leaves; data were corrected for decay of the barium sulfate standard to give absolute radiometric data (Allen and Richardson, 1971).

The method of Levitt and Zaken (1975) was used to measure percent of leaf volume according to the following formula:

$$\%I = \frac{\Delta W_L}{W_i} \times 100,$$

where I = percent of leaf volume occupied by intercellular space, W_i = weight of leaf after vacuum infiltration with water, and ΔW_L = increase in leaf weight after water infiltration.

Student's "t" test was applied to means of each of the physical measurements made on the five leaves. (The data were pooled over the 4 days to form a single data set.) Also, the physical measurement data were correlated with the spectral measurements and partial regressions were calculated at the 0.45-, 0.55-, and 0.65-μm WLs (Steel and Torrie, 1960).

Results and Discussion

Relatively early studies (Willstätter and Stoll, 1918; Seybold, 1932) and more recent investigation (Hoffer and Johannsen, 1969; Knipling, 1970; and Woolley, 1971) stimulated research on the use of spectral measurements to quantitatively measure physical and chemical characteristics of plant leaves, such as data given in Table 1. For example, reflectance measurements made at the 0.55-μm wavelength (WL) may be useful to evaluate the leaf total chlorophyll concentration of crop plants (Thomas and Gausman, 1977). However, differences in characteristics between sun and shade leaves (Sifton, 1945; Esau, 1965; Sharma and Sen, 1971) as affecting leaf spectral properties were not considered extensively. Nonetheless, sun leaves of the Valencia orange tree had a differ-

[1] Mention of a company name or trademark is for the reader's benefit and does not constitute endorsement of a particular product by the USDA over others that may be commercially available.

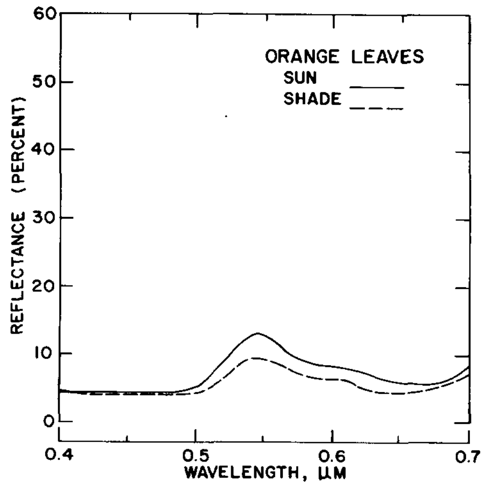

FIGURE 1. Reflectance spectra of upper surfaces of sun and shade leaves of Valencia orange trees.

ent effect than shade leaves on light reflectance within the 0.45–0.75-μm portion of the visible spectrum. For example, at the 0.55-μm green light reflectance peak, shade leaves with more total chlorophyll concentration (Table 1) had less reflectance than did the sun leaves (Fig. 1) with less chlorophyll.

The reflectance of Valencia orange sun leaves but not its shade leaves was negatively linearly correlated (r from -0.42^a to -0.47^a) with total chlorophyll concentration at the 0.45-, 0.55-, and 0.65-μm WLs (Table 2). Surprisingly, statistically significant linear correlation and β coefficients were found for the association of sun leaf mesophyll air volume with reflectance measurements made at the 0.45-μm WL, but not for shade leaves. Theoretically, this may have been caused by differences in visible light scattering and absorption phenomenon in the relatively compact mesophyll of the sun leaf as compared with the more lacunose mesophyll of the shade leaf. But this does not explain why much lower coefficients were found at the 0.55- and 0.65-μm WLs.

Shade leaves from Valencia orange trees were significantly ($p = 0.01$) more succulent, larger in area, and thinner than sun leaves (Table 1). Moreover, shade leaves had a larger mesophyll air volume and total chlorophyll concentration than sun leaves, which agrees with the work of Sharma and Sen (1971) and Sifton (1945) and has implications in the relation of internal leaf area to cellular CO_2 resistance (Larcher, 1945; Nobel, 1977; Boardman, 1977; Sinclair et al., 1977). It seems, therefore, that shade leaves in a plant canopy have the inherent potential (more air space and chlorophyll than sun leaves) to conduct photosynthesis at low light intensity (Nobel, 1977).

Leaf water content slightly influenced the reliability of reflectance measurements of Valencia orange leaf chlorophyll content (Gausman et al., 1975). Our study also indicated that this may have occurred for both sun ($r = -0.44^a$) and shade ($r = -0.50^a$; $\beta = 0.64^a$) leaves

TABLE 1 Means and Differences in Reflectances at Three Wavelengths in Total Chlorophyll Concentration, Air Volume, Water Content, Thickness, and Area per Leaf of Shade and Sun Leaves of Orange Trees

	SHADE	SUN	DIFFERENCE
Total chlorophyll (mg/g)	5.50	3.26	2.24[a]
Air volume (%)	27.02	20.98	6.04[a]
Water content (%)	63.28	57.76	5.52[a]
Thickness (mm)	0.23	0.26	− 0.03[a]
Area per leaf (cm^2)	74.79	10.85	63.94[a]

[a]Significant statistically, $p = 0.01$, according to Student's "t" test.

TABLE 2 Linear Correlation (r) and Partial Regression (β) Coefficients for the Effects of Leaf Total Chlorophyll Concentration, Air Volume, Water, and Thickness on the Reflectance of Citrus Sun and Shade Leaves at the 0.45-, 0.55-, and 0.65-μm Wavelengths

	Sun Leaves		Shade Leaves	
Factor	r	β	r	β
		0.45-μm Wavelength		
Chlorophyll	-0.45^a	-0.41	-0.02	0.13
Air volume	0.56^b	0.56^a	-0.20	0.29
Water	-0.44^a	0.14	-0.50^a	0.64^a
Thickness	-0.04	0.17	0.30	0.003
		0.55-μm Wavelength		
Chlorophyll	-0.47^a	-0.40	-0.30	-0.40
Air volume	0.19	0.12	0.12	-0.21
Water	-0.03	0.09	0.33	0.53
Thickness	-0.50^a	-0.36	-0.07	0.11
		0.65-μm Wavelength		
Chlorophyll	-0.42^a	-0.43	-0.29	0.23
Air volume	0.23	0.25	0.19	0.12
Water	-0.08	0.22	-0.06	0.01
Thickness	-0.32	-0.12	0.23	0.18

[a] Significant statistically, $p = 0.05$.
[b] Significant statistically, $p = 0.01$.

(Table 2). However, the interaction of leaf water content with leaf chlorophyll concentration and its quantitative effect on visible light reflectance needs intensive study.

We expected that leaf thickness might greatly influence reflectance, because it would affect the visible light scattering pathways (Willstätter and Stoll, 1918) within the leaf mesophyll. But a significant coefficient ($r = -0.50^a$) occurred only at the 0.55-μm WL (Table 2); sun leaves were 0.03 mm thicker than shade leaves (Table 1), however.

Conclusion

The visible light reflectance as well as leaf chlorophyll concentration, mesophyll air volume, water content, and thickness, of sun and shade leaves of orange trees was significantly different. Therefore, the influence of shade and sun leaves on visible light reflectance/absorptance of at least Valencia orange tree canopies and probably other species should be considered in modeling reflectance and growth of vegetative canopies.

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